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Growth dynamics of Collembola *(Folsomia candida)* and a fungus *(Mucor plumbeus)* in relation to nitrogen availability in spatially simple and complex laboratory systems

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With 3 figures

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1. Introduction

Fungal tissues are an important dietary component of many invertebrates in decomposer communities (MARTIN, 1979) though the relative proportions of hyphae and higher plant materials ingested depend upon the size of the animal and its feeding habits (ANDERSON, 1975). The mites and Collembola have small body sizes which facilitiate selective feeding in litter and soil microhabitats and most species in these groups, particularly Collembola, are predominantly mycophagous.

There are estimations that as much as 86% of the fungal production is consumed by mesofauna in some forest soils (MCBRAYER *et al.*, 1974; TADROS & VARNEY, 1983), though MITCHELL & PARKINSON (1976) suggest that this is a substantial overestimate, but never-the-less it has been demonstrated that grazing can alter the balance of fungal and bacterial biomass in microsites, influence fungal growth and activity and alter the distribution and abundance of fungal species under field and laboratory conditions (ADDISON & PARKINSON, 1978; HANLON & ANDERSON, 1979; NEWELL, 1984 a, b; VAN DER DRIFT & JANSEN, 1977, VISSER, 1985).

The mechanisms underpinning these responses have not generally been investigated but conditions affecting the relative growth rates of the mycelium and Collembola populations will be of central importance; particularly the quality of the resource on which the fungus is growing and the physical structure of the habitat.

Fungal growth rates are affected by the carbon and nutrient supplies in the resources being exploited, though the response is not necessarily linear (PARK, 1976), and this influences susceptibility to grazing. For example, HANLON (1981) showed that Collembola inhibited the growth and activity of *Botrytis cinerea* (PERS. *ex* FR.) under nutrient limited conditions but had the reverse effect in cultures with higher media concentrations. Furthermore, the consumption rates by the Collembola were influenced by the age of the culture, slow growing and senescent tissues being less preferred, as well as the nutritional state of the fungus (LEONARD, 1984a). BOOTH & ANDERSON (1979) also showed that growth rates and egg production of *Folsomia candida* (WILLEM) were affected by the nitrogen concentration in the culture media of *Coriolus versicolor* (L. *ex* FR.) QUEL.

Habitat structure has been considered as a variable affecting the dynamics of protozoan/bacteria, nematode interactions (ANDERSON & COLEMAN, 1977; ELLIOT *et al.*, 1980) but most of the laboratory experiments on collembolan grazing effects on fungi have been carried out on planar surfaces.

Thus there is evidence of positive and negative feedbacks between fungi and Collembola according to culture conditions but no studies of these interactions have been performed in structurally complex systems. Hence, rather than set up experimental systems containing litter materials which represent largely uncontrolled habitat variables, artificial substrates

were used to investigate the influence of physical complexity on the dynamics of collembolan/fungus interactions. The validity of this approach is illustrated by PARR *et al.* (1963, 1967) and ANDERSON & COLEMAN (1977) who showed that growth characteristics of organisms in three-dimensional matrices differed significantly from those in experiments on agar plates or other simple growth surfaces.

2. Materials and methods

2.1. Collembola

Stock cultures of the Collembola *Folsomia candida* (WILLEM) were maintained as described in LEONARD (1984a). The problem of introducing a heavy contaminent load into gnotobiotic systems with the original inoculum of Collembola was avoided by surface-sterilising the Collembola. The conclusions of many investigations have been complicated by the presence of unknown microbes carried into the experimental systems by the animal component (eg. HANLON & ANDERSON 1979; PARKINSON *et al.* 1979; VISSER *et al.* 1981). One of the simplest methods (having no adverse effects on the Collembola or residue problems) is their immersion in 1% sodium hypochlorite ('Chloros') solution (eg. MILLS & SINHA, 1971). This treatment, however, proved to be insufficient to destroy all the bacteria and fungi present on their external surfaces and an alternate method was developed. Starved Collembola were immersed in 1% Chloros solution for 10 minutes, rinsed in sterile distilled water and held for 3 days on sterile bases containing a few pellets of sterilised yeast. They were then reimmersed in sterilant, rinsed, and five animals were added to each experimental unit.

2.2. Fungus

For inclusion in the experimental units the fungus had to fulfil certain prerequisites, namely:
(a) Palatability to the Collembola.
(b) Growth response to the nitrogen resource employed.
(c) Suitability as a dietary resource.

Several species were assayed for these characteristics and *Mucor plumbeus* (MICH. *ex* FR.) was chosen as the experimental fungus. Full details are given in LEONARD (1984b).

2.3. The experimental system

The chemically defined medium of LEVI & COWLING (1969), modified by the inclusion of glucose ($20\ g \cdot l^{-1}$) was used throughout. Asparagine monohydrate, added as the sole nitrogen source, was calculated to give final nitrogen concentrations of 2, 20 and 200 $mg \cdot l^{-1}$ for the longer term experiments and a range of between 2 and 200 $mg \cdot l^{-1}$ for the nine week consumption study. The culture solutions were adjusted to *p*H 5.5 (if required), autoclaved and stored in sealed medical flats ready for use.

The first series of experiments were conducted using glass micro-beads (approximately 150 µm diameter) to produce a simple homogeneous matrix (designated two-dimensional, 2D), which provided spatially unlimited contact between the fungal and collembolan components of the system.

The glass micro-beads, as supplied by the manufacturer, required rigorous cleaning to remove surface alkalinity. PARR & NORMAN (1964) washed their beads with dilute HCl, whilst other investigators have used 'Pyroneg'. Neither of these methods proved satisfactory for reducing the surface alkalinity of the beads, so the method suggested by TAYLOR (in PARKINSON *et al.*, 1971) was adopted: the beads were soaked in 2M nitric acid for 48 hours with occasional stirring, the acid was then decanted and the beads washed under running water for several hours. When the *p*H of the effluent water equalled the influent, the beads were further washed in ten successive changes of distilled water and, if there was no change in *p*H when left overnight, the water was decanted and the beads were dried for storage

in stoppered bottles. If a change in *p*H was noted in the final stage the entire washing procedure was repeated. Subsequent cleaning of used beads was carried out in dilute HCl but where there were signs of heavy contamination the above procedure was repeated.

Measured volumes (15 ml) of dried beads were added to (190 ml capacity) milk bottles which were plugged with cotton wool and capped with foil. The bottles and contents were then sterilised by autoclaving and allowed to dry at room temperature. Aliquots of the defined liquid media were added aseptically; 5.6 ml was found sufficient to fill the available pore spaces but insufficient to "fluidise" the matrix. Finally the units were inoculated with a small plug of agar from the periphery of the fungal clony growing on water-agar plates. The units were then incubated at room temperature to allow a mat of fungal mycelium to develop and, after seven days has elapsed, five surface-sterilised Collembola were added to each grazer unit. The bottles were held in trays containing moist sand and enclosed in large polythene bags to maintain humidity.

The second series was conducted using a complex 3-dimensional (3D) matrix with pore spaces of differing sizes. These units were constructed using Lessing rings (ceramic tubes 20 mm × 10 mm diameter with a diagonal plate through the centre) precleaned as described above. Similar volumes of rings were added to each bottle, autoclaved and dried. Aliquots of the defined liquid media (similar to those used in the 2D units) were added aseptically to each bottle. The volume of liquid was sufficient to cover the surfaces without leaving any free liquid in the bottom. The inoculum was introduced as a hyphal suspension in the liquid media and experimental animals were added after seven days had elapsed.

2.4. Size classes

The recording of total numbers in a population yields little information regarding the processes being monitored. However, analysis of age structure in soil arthropod populations presents many difficulties that have been pointed out by a number of investigators (eg. HEALEY, 1971). As a consequence, data on the demography of soil arthropods is rare, although quantitative knowledge regarding these processes is essential in the understanding of decomposition.

F. candida has an exceptionally high intrinsic population growth rate (GREGOIRE-WIBO & SNIDER, 1977), so the recording of total numbers may be misleading when assessing their impact over time due to the disproportionate number of hatchlings present at any point in time. In order to provide greater insight into population dynamics the experimental animals were divided into two size classes. Individuals less than five days old and less than 0.5 mm in body length were called "small" and gave a measure of the fecundity and status of the resident population. The second grouping ("large") included all other individuals up to maximum size which represented the successful recruitment to the grazing population from the innumerable hatchlings that had been active during the periods between monitoring. Full details are included in LEONARD (1984b).

2.5. Monitoring

Five units were destructively sampled weekly (10 in the case of the consumption study) and then at four-weekly intervals. In both the 2D and 3D units the Collembola were enumerated and classified into the two size classes. Sampling was carried out by flooding the units with distilled water and stirring gently, the Collembola, having a hydrofuge cuticle, collected on the water surface and were removed with a small net.

The fungal component of the glass bead units was separated from the matrix using an MSE homogeniser (operating at 6000 rpm for 1 minute). The beads were allowed to settle for 30 seconds and the supernatant filtered through pre-weighed Whatman no. 52 quantitative filter papers, held in a Buchner funnel under low vacuum; the beads were further washed using distilled water to recover all the fungal material. The filter papers were wrapped in foil and dried at 105 °C to constant mass.

The fungal component in the Lessing ring matrix was retrieved by washing the individual rings in a jet of distilled water onto the filter papers, which were dried and weighed as before. The matrix material was cleaned and reused.

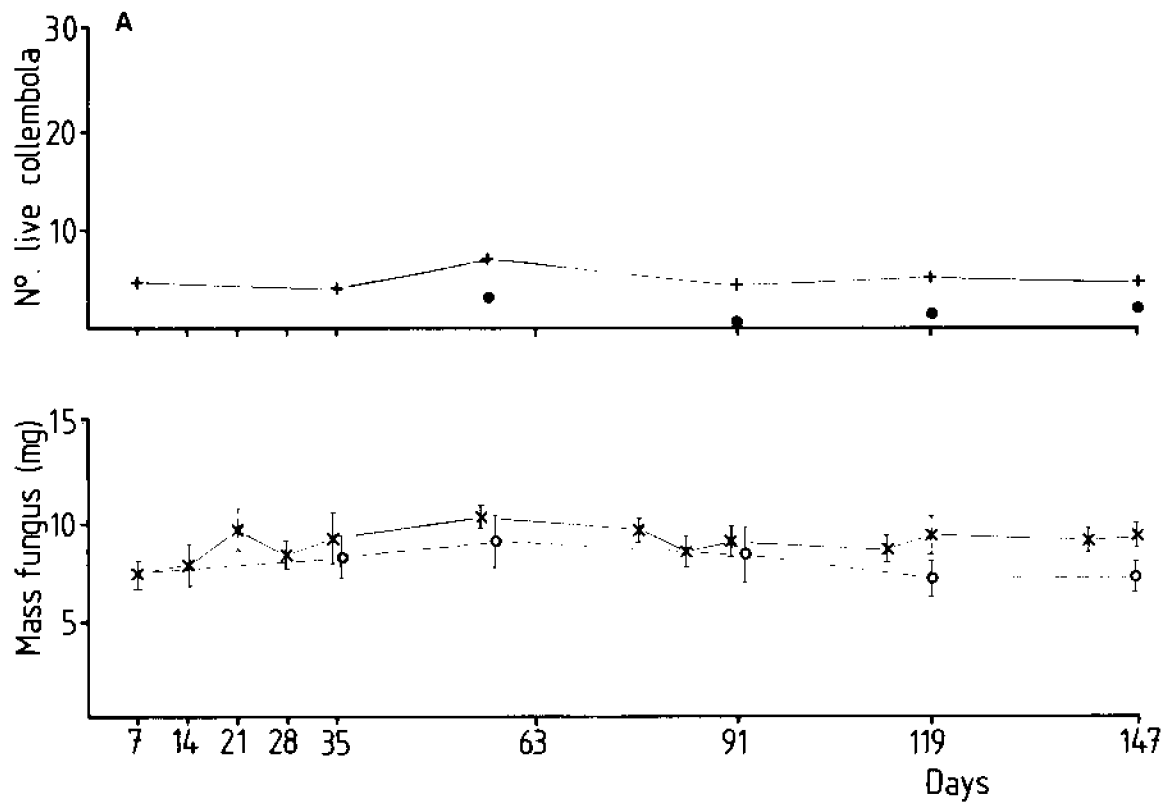


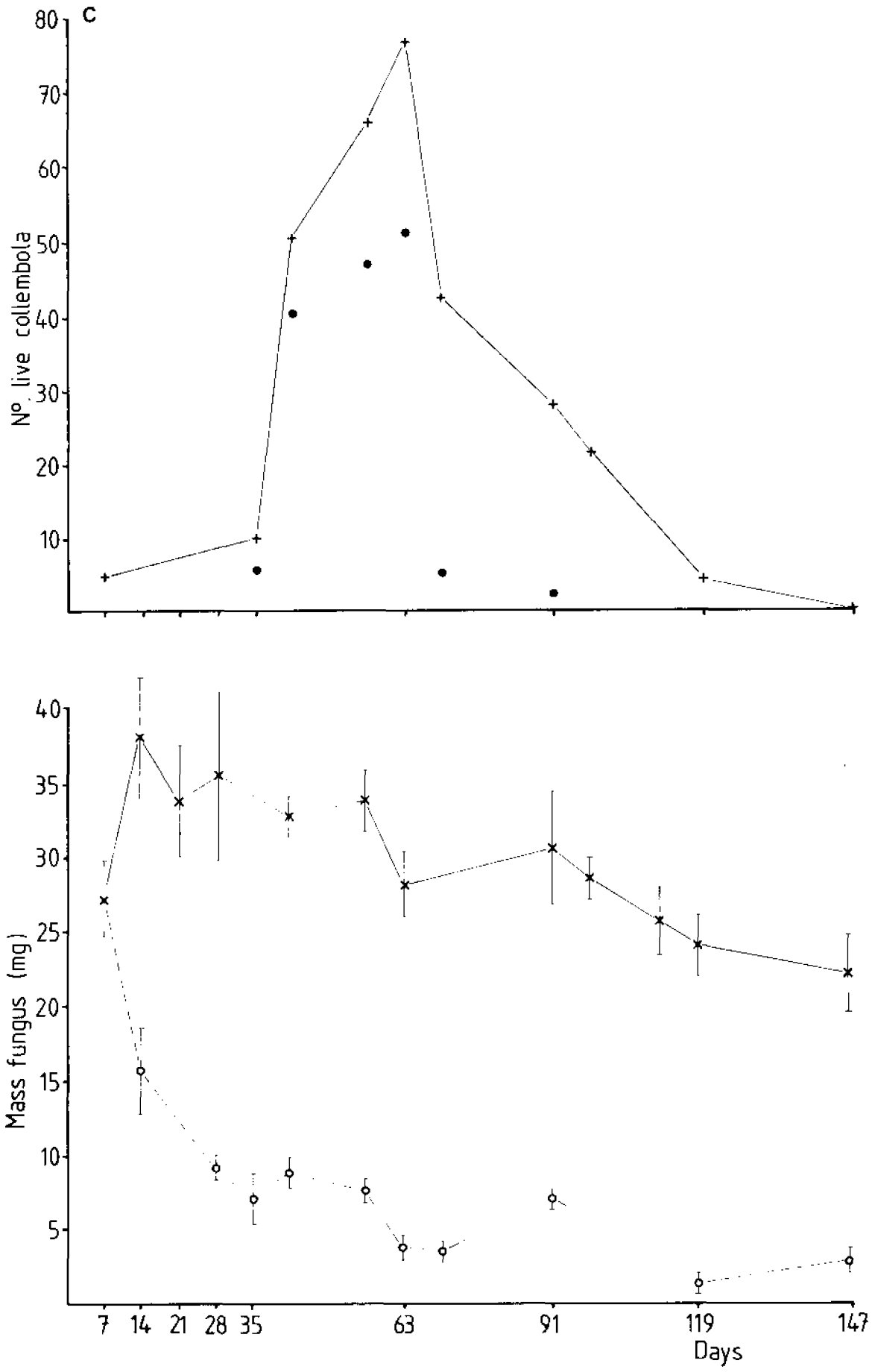
Fig. 1. Standing crops of fungus (mg dry mass) recovered from grazed (○) and ungrazed (×) glass containing: (A) 2 mg l^{-1} Nitrogen, (B) 20 mg l^{-1} Nitrogen, (C) 200 mg l^{-1} Nitrogen. Collembola added on day 7 ('○' = young; animals less than three days old).

3. Results

3.1. Interactions in the simple systems

The grazing interaction between the collembolan and fungal components within the simple, homogeneous systems, and the influence of changes in the level of the nitrogen resource are shown in figure 1.

At the lowest level of added nitrogen (2 mg · l^{-1}) the fungal and collembolan populations were apparently in equilibrium with fungal standing crops showing little change and the number of Collembola recovered over the experimental period from each bottle remaining around five. At 200 mg · l^{-1} the Collembola population exhibited a bell shaped response, with an initial lag phase followed by an exponential increase in numbers (figure 1c). As a result, the fungal standing crop available to the animals was rapidly depleted to a level appearing insufficient to maintain the increased numbers of grazers, which, at nitrogen concentrations above 2 mg · l^{-1}, subsequently declined to extinction.



micro-bead (2D) units and the changes in the number of Collembola recovered alive from units Results are expressed as mean values +/−1 SE (Error bars maybe obscured by the symbols).

The amount of fungal standing crop (growing on a range of nitrogen concentrations) consumed by the Collembola by day 35 (28 days grazing) was determined by subtracting the hyphal mass in the grazed units from that in the ungrazed units. Day 35 represented a point midway between the addition of, and the recruitment to, the grazing population. Analysis of residuals showed there to be a log/log relationship with a marked correlation ($P < 0.01$) between the nitrogen concentrations of the media being exploited by the fungus and the reduction in its standing crop through grazing. Continued monitoring showed that maximum population size was attained by day 63 with analysis showing a high, linear correlation ($P < 0.01$) between nitrogen concentrations in culture and the level of recruitment to the grazer population twenty-eight days later (fig. 2.).

3.2. Interactions in the complex systems

The grazing interactions between the two components within the complex systems are shown in fig. 3. At the highest nitrogen level ($200\ mg \cdot l^{-1}$, fig. 3c.) the interaction was very similar to that in the simple system. At lower nitrogen concentrations, however, the

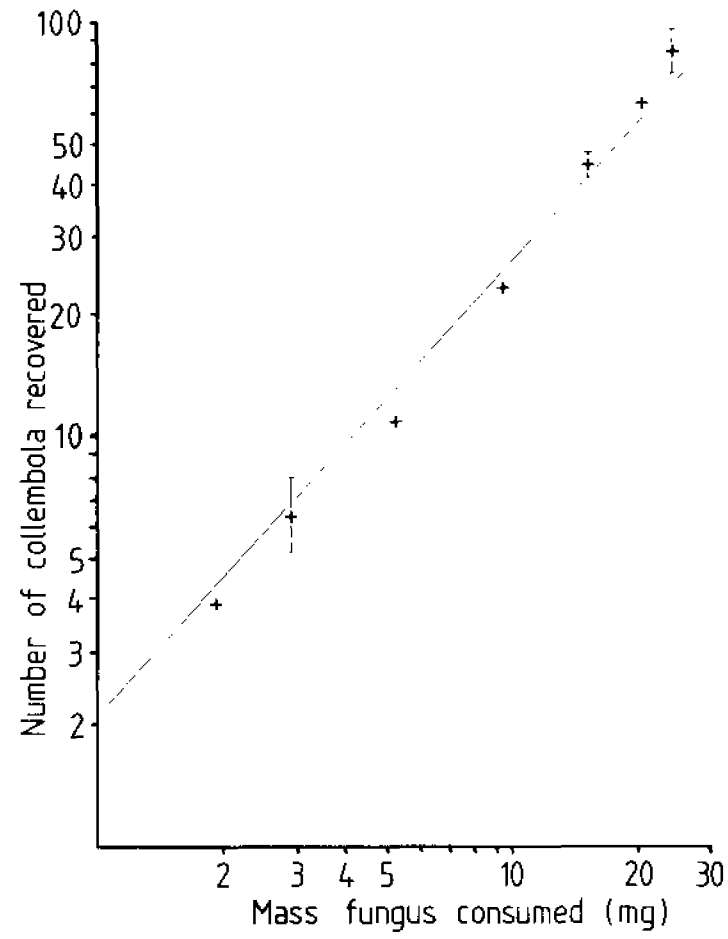


Fig. 2. Summary of data showing the number of Collembola recovered alive on day 63 against the dry mass (mg) fungus consumed by day 35 in the glass micro-bead units.
Results are expressed as mean values +/−1 SE. Line of best fit generated by regression analysis ($r = 0.9965$, $df = 5$, $P < 0.01$).

patterns were dramatically reversed. At both 2 and 20 mg · l^{-1} nitrogen, grazing resulted in an enhancement of fungal recoveries over those from ungrazed units. Further, the increased numbers of grazers appeared to be maintained over longer periods. In both cases there was some element of equilibrium in the interaction.

4. Discussion

Results of this experiment exhibit the classical phenomenon described by GAUSE (1934) and HUFFAKER (1958) that small-scale spatial heterogeneity reduces the extremes of potentially unstable limit cycles of interacting species and facilitates their co-existence. However the time course and response of the system were complicated by the effect of culture conditions on both the fungus and the Collembola.

As the availability of nutrients to the fungus was increased under the different culture conditions there was an increase in the quality as well as the quantity of fungus as an exploitable food resource. Analysis of fungi grown on different concentrations of available nitrogen has shown that the complement of amino acids as well as total protein responded to improved culture conditions (BOOTH, 1979; DOWDING, 1976, 1981). Further, characteristics of the cell wall also vary depending upon the nutrients available and the age of the culture (SHARMA *et al.*, 1977). LEONARD (1984a) showed that these factors influenced their value as a food resource: Collembola strongly favouring high quality food resources when offered single fungal species grown on a range of nutrient media. This improved food quality has profound effects on the population dynamics of Collembola (BOOTH & ANDERSON, 1979).

In the two-dimensional systems containing low concentrations of nitrogen (2 mg · l^{-1}, little fungal material was available for exploitation by the grazing animals. Little of this low quality food resource was consumed and there was no real change in the numbers of animals over time. This is a valuable observation, especially in relation to the demography of the grazer population, because food scarcity is considered an important source of stability through reducing the amplitude of population fluctuations (JOOSSE & TESTERINK, 1977a; SMITH, 1972). Moreover, food limitation has also been shown to increase the longevity of

soil micro-arthropods, thereby improving their chances of survival when poor conditions prevail (JOOSSE & TESTERINK, 1977b; VERHOEF & LI, 1983). This stability was lost as nitrogen levels available in culture increased. More fungal resource was available to the Collembola and the greater quantity and quality elicited rapid population increased with an eventual over-exploitation of the finite resource and the extinction of the grazer.

In all cases the maximum population size was attained by day 63: the result of eggs laid prior to day 40: studies having shown that embryonic development takes around 20 days at 20 °C, the ambient temperature of the experiment (GREEN, 1964; SNIDER, 1973). A marked correlation was found between this number of Collembola and the level of nitrogen available in culture. Since the fungus was the sole food resource supporting animal production the differences between the standing crops of fungus recovered from the grazed and ungrazed systems gave a measure of the amounts ingested by the Collembola, though it is recognised that this also reflects the reduction in standing crop due to the disruption of mycelia and other inhibitory effects attributable to grazer activity. The log/log basis of the relationship between consumption and recruitment implies that quantity as well as quality elicits enhanced egg production and, although individuals have a limited capacity to feed, the population as a whole soon expands to exploit the resource. Thus, in the absence of competition through imigration Collembola are able to fully exploit high quality food sources; but if such a source is constrained by space the result would be a single limit cycle.

The introduction of small-scale heterogeneity into the high nitrogen availability systems reduced the severity of the grazing effects but the large increase in animal numbers still depleted their fungal resource to a low level, as in the two-dimensional systems, and the grazer population declined. Conversely in the three-dimensional low nitrogen systems there was no decline in the number of grazers; moreover, the result of grazing was an increase in the fungal standing crops present. Small-scale spatial heterogeneity had conferred a great deal of stability on the grazing interaction; the small pore spaces inherent in the matrix probably acted as refuges for eggs from oophagy and the fungus from over-grazing.

How do the interactions observed in these simple laboratory systems relate to more complex litter systems and, ultimately, the field? Work by INESON *et al.* (1982) showed that the interaction in litter systems may be considered a mix of responses in the two and three dimensional systems. The fungal standing crops initially increased under low grazing intensities but as the pressure of animal numbers increased the hyphal mass declined. However, unlike the two-dimensional systems, the number of Collembola remained reasonably stable after their initial increase. Other work has shown that further to stimulation or inhibition being real consequences of the interaction, grazing can play an important role in the distribution and structure of the fungal community through space and time (NEWELL, 1984 a, b; VISSER *et al.*, 1981).

Thus both inhibition and stimulation of fungal activity have been demonstrated. It may therefore be argued that in the soil/litter system an increase in heterogeneity of microhabitats due to the reduction in litter particle size (with attendant decrease in pore size), and the penetration of roots and plant debris by fungal hyphae, could provide a mechanism by which young colonies and actively growing hyphal tips of later successional fungi are protected from grazing.

The main conclusion that may be reached from this experiment is, however, that even in the highly simplified three-dimensional matrix interactions are very complex and will depend on the quality of the decomposing material, the degree of processing by other organisms and the length of time that the matrix is maintained.

5. Acknowledgements

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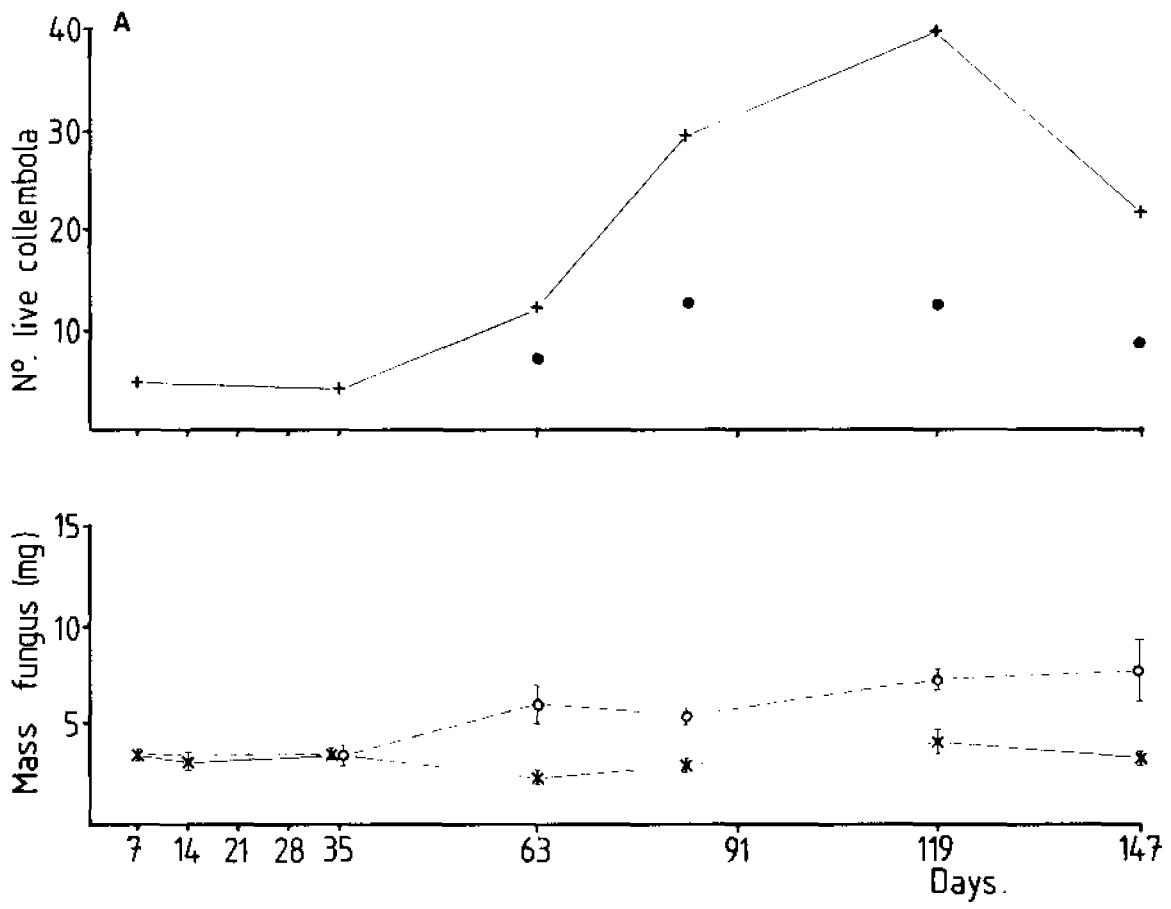

Fig. 3. Standing crops of fungus (mg dry mass) recovered from grazed (○) and ungrazed (×) complex (A) 2 mg l^{-1} Nitrogen, (B) 20 mg l^{-1} Nitrogen, (C) 200 mg l^{-1} Nitrogen. Details as figures 1 A–C.

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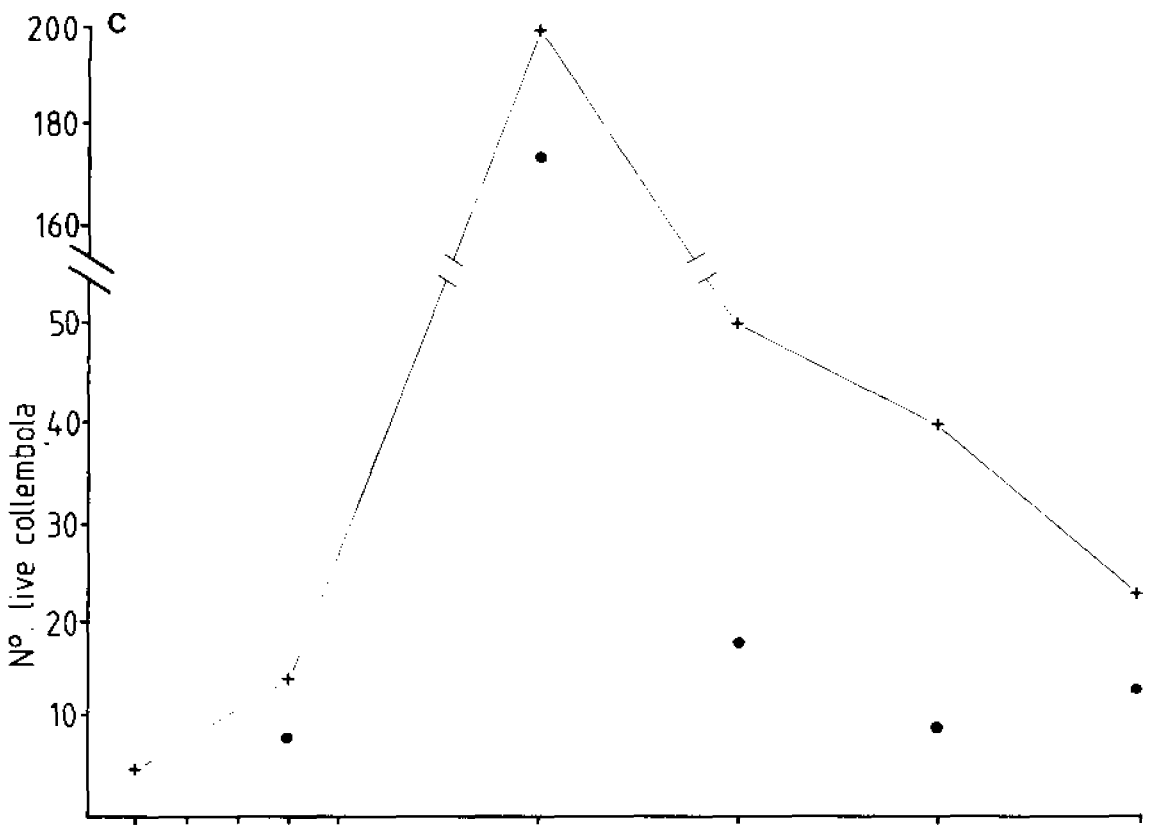

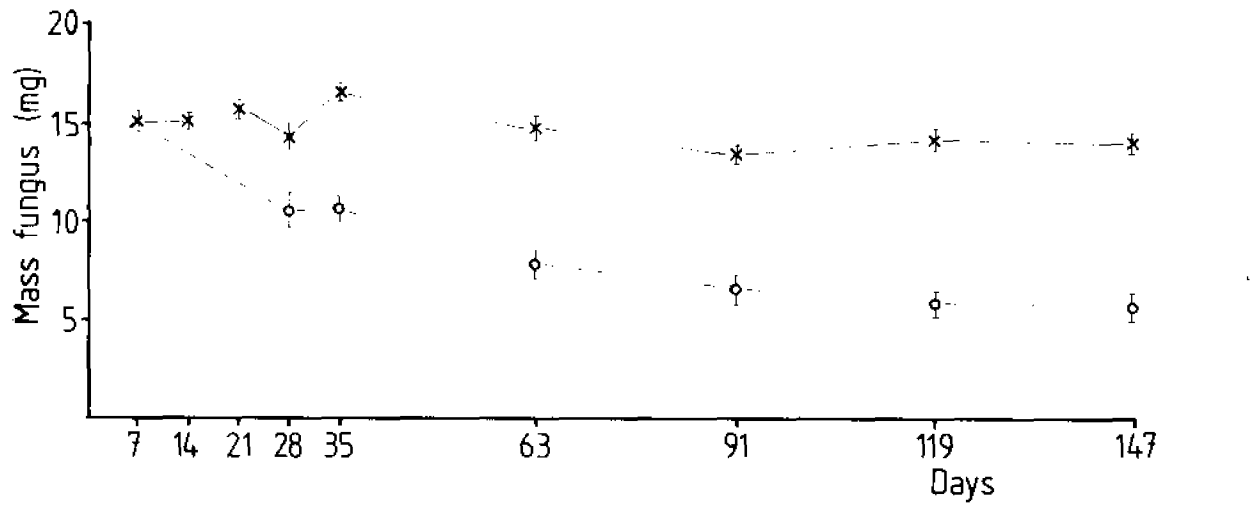

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Synopsis: *Original scientific paper*

LEONARD, M. A., & J. M. ANDERSON, 1991. Growth dynamics of Collembola *(Folsomia candida)* and a fungus *(Mucor plumbeus)* in relation to nitrogen availability in spatially simple and complex laboratory systems. Pedobiologia **35**, 163–173.

Laboratory systems were developed to study the interactions between a collembolan and a fungus in relation to different levels of available nitrogen (2, 20 and 200 mg l^{-1}) within spatially simple systems (glass micro-beads) and complex systems (ceramic cylinders). In the spatially simple systems, the cultures with 200 mg N l^{-1} showed a single limit cycle resulting in the death of the Collembola and almost complete elimination of fungal hyphae after 147 days. At concentration of 2 mg N l^{-1} the quality and quantity of fungal production was insufficient to produce a large growth response by the Collembola and both species were maintained in the system. At all three concentrations of nitrogen the decrease in fungal standing crop after 28 days grazing was correlated with recruitment to the Collembola population 28 days later.

The use of ceramic cylinders to produce a more complex, spatially heterogeneous habitat, resulted in a reversal of the interactions at 2 and 200 mg N l^{-1} observed in the simple system. In the complex system higher numbers of Collembola were maintained and the recovery of fungal biomass was also higher in the ungrazed cultures. The importance of nutrient availability and spatial heterogeneity in micro-arthropod/fungal interactions is discussed.

Key words: collembola populations, fungal biomass, growth dynamics, spatial heterogenity, limit cycles.

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